

The University of Chicago

STRUCTURE OF PALEOZOIC SEEDS
OF THE TRIGONOCARPALES

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

1936

By
CHARLES LEE DEEVERS

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STRUCTURE OF PALEOZOIC SEEDS OF THE TRIGONOCARPALES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 476

CHARLES L. DEEVERS

(WITH THIRTY-SIX FIGURES)

Introduction

Much interest has been shown in the seeds of the Paleozoic era since the discovery that many of the fern-like leaves of that period belong to the gymnospermous Cycadofilicales as well as to the true ferns. BRONGNIART grouped these seeds into two classes, the *Platyspermae* and the *Radiospermae*. SEWARD classified the 29 genera of these seeds into three orders, the *Lagenostomales*, the *Trigonocarpales*, and the *Cardiocarpales*. The *Lagenostomales* and *Trigonocarpales* include BRONGNIART's *Radiospermae*, and the *Cardiocarpales* his *Platyspermae*. These Paleozoic seeds show affinities with the seeds of the cycads.

More than 65 species of *Trigonocarpus* have been described during the past hundred years, mainly as seed casts. The structural details of scarcely more than half a dozen have been given. FIEDLER (3), KRICK (4), and SEWARD (8) have summarized the literature of this group.

Six species of the *Trigonocarpales* are described in this paper, five of them belonging to the genus *Trigonocarpus*. Following the suggestion of SCOTT and MASLEN (10), the term *Trigonocarpus* has been used rather than *Trigonocarpon*, which was used by WILLIAMSON and NEWBERRY.

The specimens of *Trigonocarpus* studied were collected at Petit Jean Mountain, 12 miles southwest of Morrilton, Arkansas, in Cedar Creek Canyon, about three-fourths of a mile below the waterfall of the same name. They were found literally by the bushel in huge boulders which had fallen down from the eastern side of the cliff. The seeds occur in a hard, gray sandstone in a layer about 3 feet thick which overlies a thick bluish shale. This sandstone layer is 100

feet or so above the bottom of the canyon, and approximately 200 feet below the edge of the cliff. The same stratum appears again on the opposite side of the mountain, where these specimens are numerous. The geologic horizon is upper Atoka, about 150 feet below the Hartshorn sandstone which caps Petit Jean Mountain. The Atoka and the Hartshorn correspond to the Pottsville in age, and therefore represent the Lower Pennsylvanian strata (2). One specimen of the *Trigonocarpales* was collected by Mr. N. J. Gillett in the Strip Mine of the Northern Illinois Coal Company at Wilmington, Illinois. It was found above coal no. 2, which forms the basis of the Allegheny group of the Pennsylvanian system in Illinois.

For detailed studies of internal structure and other anatomical features of these casts, sections of the material were made by means of the diamond saw and carborundum powder. After carefully polishing the faces of the sections, a thin film of canada balsam was spread over them, and they were examined by reflected light. Thin sections of *Trigonocarpus* failed to show any cellular detail, so descriptions are based mainly on surface views. A total of 150 specimens was available, and of these approximately 100 were sectioned. Thin sections and peels were made of the Illinois specimen by the use of the celloidin film method. Histological details were found in these.

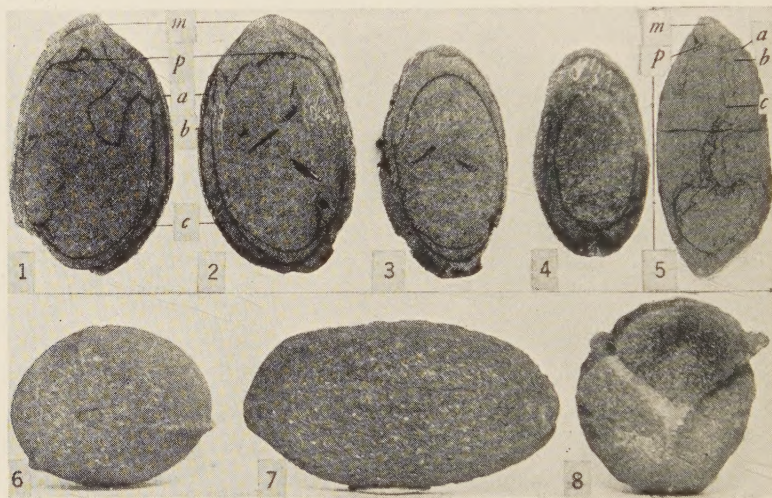
Among the material available there are specimens representing at least two previously described species. These are *Trigonocarpus dawesi* Lindley and Hutton and *T. noeggerathi* Brongniart. The same species have been described by several investigators from material obtained both in Europe and America. The remaining species are considered to represent three new species and one new genus and species. None of the specimens of *Trigonocarpus* shows any cellular details, but certain structural features are evident from the regular occurrences of carbonized remains of membranes.

None of the seeds upon which this investigation is based was found directly attached to other plant organs, but several fragments of stems and pith casts of *Cordaitea* were found associated with them. Near the locality where the seeds were found, many casts of *Stigmaria ficoides*, some species of *Calamites*, and a few stems of *Lepidodendron* were present. The seeds show no evidence that they were transported or stream worn; they appear to have been fossilized where they fell.

Description of species

Trigonocarpus dawesi Lindley and Hutton (figs. 1-8, 12)

Fifty seeds of this species were investigated, and 35 of them were sectioned. They are of large size, varying in length from 3.5 to 5.5 cm., oval in shape, nearly circular in cross section, and from 1.7 to 2.7 cm. thick. They bear on the surface three nearly equidistant salient ridges or wings. About half of the specimens are winged



FIGS. 1-8.—Fig. 1, *Trigonocarpus dawesi* Brgt., nearly median longitudinal section: *m*, micropylar end of cast; *p*, pollen chamber with top broken and resting on megaspore membrane; *a*, darker layer, the sclerotesta; *b*, carbonized remains of inner flesh; *c*, megaspore membrane-nucellus remains. Figs. 2-4, serial sections from median to outside of same cast. Fig. 5, median longitudinal section of another cast of same species; megaspore membrane-nucellus remains crushed and invaginated. Figs. 6-8, *T. dawesi* Lindley and Hutton: 6, view of basal end showing foramen partly filled with carbonized remains of vascular tissue; 7, side view showing one of three ridges; 8, micropylar end with part of wing still intact at upper right. Note tendency that many specimens have of splitting into three valves.

(fig. 8) and half bear ridges only (figs. 6, 12). These wings and ridges extend the entire length of the seed, from about 5 mm. above the foramen to the micropyle. The wings are approximately 1 mm. thick, and increase in width from near the foramen to a point about 1 cm. from the micropyle, where they are 4 to 5 mm. wide. The ridges are uniform in size.

The sclerotesta is evident in many of the sections as a darker layer, the outermost layer of the cast, and is about 1 mm. in thickness (fig. 1 *a*). It is also evident in the winged specimens (fig. 8) and probably in those having ridges (fig. 12). In many of the specimens the sclerotesta is sharply pointed in the micropylar region; in others it is less pointed or broken. The basal end is rounded, and near its center is a conspicuous foramen (fig. 6).

The inner flesh is represented by a thin carbonized membrane just inside the sclerotesta (fig. 1 *b*). This membrane extends over the entire inner part of the seed from the basal disk to the micropyle, although it is often broken and crushed (fig. 5). In figures 1-4 it is shown in about its original position.

There is no indication of a nucellus separate from the megaspore membrane and the pollen chamber. The latter is evident in many of the specimens as a truncated cavity about 3 mm. high, and in the best specimen is 1 cm. broad at its base (fig. 1 *p*). The membrane inclosing this structure is broken and shrunken, as are the other membranes. The vascular organization is shown poorly, except as a carbonized mass in the foramen at the base of the seed (fig. 6). The nucellus-megaspore membrane is much more prominent than the other membranes; apparently the nucellus had a definite vascular system which is carbonized and included in this complex.

The megaspore membrane appears relatively thick, probably because the nucellar remains are also in contact with it. It is in about its original position in figures 1-4, where it surrounds the cavity previously occupied by the megagametophyte. The megaspore membrane usually is invaginated as seen in figure 5.

The winged specimens represent casts of forma beta as designated by ARBER (1); that is, those which have the sclerotesta as the outermost part. It is possible that the ridged specimens represent forma gamma casts (casts of the inner portion of the sclerotesta only). In the Arkansas material both the ridged and the winged specimens show a foramen at the base, and a darker layer about 1 mm. thick as the outermost layer of the cast. This darker layer is the sclerotesta. It is not known whether the sclerotesta represents the former thickness of this layer, but the sclerotesta of the known *Trigonocarpales* is somewhat less than 1-4 mm. in thickness. Usually the

wings are broken off in removing the seeds from the inclosing matrix, and the seeds have a tendency to split into three nearly equal valves (fig. 8). The question arises whether the specimens possessing wings are to be considered as belonging to the same species as those having ridges, or distinct from them. Those specimens which bear wings along the entire length of the seed closely resemble *Trigonocarpus bertholletiformis* (*T. bertholletiforme* Foster; 5, pl. 42, figs. 12, 12 a); but after allowing for a degree of variation among the specimens available, it seems more probable that they are variants of a single species.

Trigonocarpus noeggerathi Brongniart (figs. 9-11, 26)

Fifty seeds of this species were studied, and about 35 were sectioned. They were not so large as those of *Trigonocarpus dawesi*. They vary in length from 2 to 3.4 cm., are ovate, and are nearly circular in cross section. In breadth they have a maximum diameter of 2 to 2.4 cm., and bear on the surface three nearly equidistant wings which extend from near the hilum to the micropyle. These wings are not so prominent as those of *T. dawesi*, and a large number of the seeds tend to break into three equal valves along the line of the wings, in the same manner as the former species.

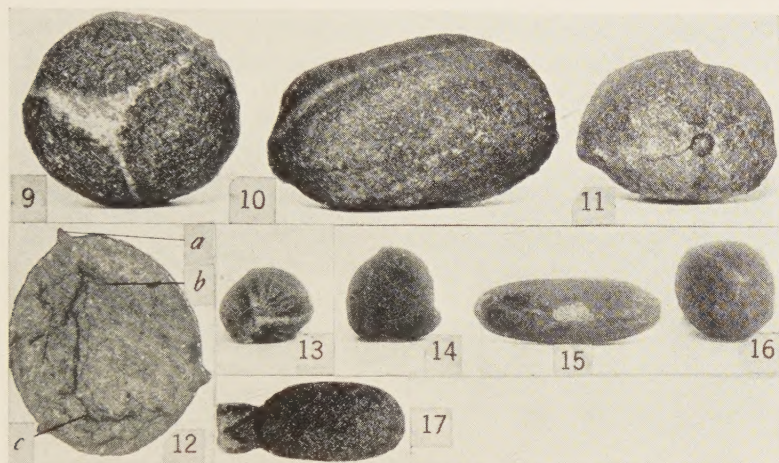
The sarcotesta is represented by a thin carbonized film uniformly thick over the entire seed; and as in the former species there is no indication of the thickness which this part of the integument may have had in the living state.

The sclerotesta is evident, as in *T. dawesi*, as a darker layer about 1 mm. in thickness. It is less pointed in the micropylar region than it is in the former species, and has a blunt appearance (figs. 9, 10). The rounded base has the foramen as has *T. dawesi* (fig. 11).

The inner flesh is represented by a thin carbonized membranous structure immediately inside the sclerotesta (fig. 26 b). This membrane extends over the entire inner part of the seed from the basal disk to the micropyle. Often it is broken and displaced.

There is no indication of the nucellus other than the megaspore membrane and the pollen chamber. Since the innermost membrane of these casts appears much more conspicuous than the membrane representing the inner flesh, it is probable that the nucellus, with its vascular tissue (9), is not separate from the megaspore membrane.

The pollen chamber is evident in many of the specimens as a truncated structure just above the megaspore membrane. The membrane about the pollen chamber is shrunken and collapsed in figure 26, and is not so large, proportionately, as the same structure in *T. dawesi*. The vascular organization is poorly shown, except as a carbonized mass in the foramen. What may have been the extent of the vascular tissue originally present is not indicated, unless the



FIGS. 9-17.—Fig. 9, *Trigonocarpus noeggerathi* Brgt., micropylar end showing three wings, or salient ridges. Fig. 10, side view, micropylar end to left, showing part of two wings. Fig. 11, basal view showing foramen partly filled with carbonized remains of vascular elements. Fig. 12, *T. dawesi* Brgt., cross section at middle of cast: *a*, one of three ridges; *b*, folded and shrunken remains of inner flesh; *c*, megaspore membrane-nucellus complex. Fig. 13, *T. costatus* sp. nov., micropylar view showing three primary ridges with about 20 smaller ones between them. Fig. 14, basal view showing characteristic splitting. Fig. 15, side view, basal end to left. Fig. 16, micropylar view showing slightly pointed apex. Fig. 17, *T. serratus* sp. nov., side view, basal end to right. Three of the six divisions of cuplike structure of summit seen at micropylar end to left.

thickness of the layer representing the megaspore membrane-nucellus includes the vascular tissue of the nucellus (10).

These casts vary considerably in size and shape. Again it is possible that more than one species may be represented in this collection, but until better preserved specimens are described it seems best to consider them as belonging to one species.

Trigonocarpus ouachitensis sp. nov. (figs. 18-25)

DIAGNOSIS.—A radially symmetrical obovoid seed, flattened at base and circular to hexagonal in cross section. Sclerotesta (length 2 cm., width 1 cm.) produced into a sharp apex, and bearing six ribs (three principal sharp angled and three less prominent). Ridges flatten out equally near the middle of the seed to form an irregular to regular hexagon at the base. Sarcotesta present only in the form of a thin carbonized membrane.

This species is represented by 33 specimens, 15 of which were sectioned. It is much smaller than *Trigonocarpus noeggerathi*, and is



FIGS. 18-26.—Fig. 18, *Trigonocarpus ouachitensis* sp. nov., basal view showing hexagonal form of sclerotesta about base. Fig. 19, side view, micropylar end to left; three of the six ridges apparent. Fig. 20, micropylar end with three major and three minor ribs; apex broken off. Figs. 21-25, serial sections from base to near the micropyle. Fig. 26, *T. noeggerathi* Brgt., near median longitudinal section: *m*, micropylar end; *a*, sclerotesta; *b*, carbonized remains of inner flesh; *c*, megaspore membrane-nucellus, much shrunken.

characterized by the seeds being of comparatively uniform size. While there is little evidence that the three principal ridges were prolonged into a micropylar tube, it is possible that this was the case. The three less prominent ribs end at the micropyle, and in many of the specimens the micropylar end is broken off (fig. 20). There is no evidence in the matrix which surrounded the casts of the presence of a micropylar tube, but it is only after well preserved structural specimens of *T. parkinsoni* were studied that this structure was found in that species (10). The base of the seed is somewhat dome-shaped, resembling in this respect the base of *T. oliveri*

Scott and Maslen (10). It differs from *T. oliveri* in that the base is not so broad, proportionately, and in tapering more sharply toward the micropyle. The base is distinctly hexagonal in most of the specimens. SALISBURY (7) thinks that *T. oliveri* has eight ridges, and that it is not a true *Trigonocarpus*.

There is little structure preserved in these specimens. The carbonized remains on the outside of the casts are apparently much thicker than in the former two species, indicating that the sarcotesta was of much greater thickness in this seed. Figures 21 to 25 show a broken, carbonized, membranous structure, which probably represents the megaspore membrane-nucellus remains. The nucellus was free to the base, and has vascular tissue present.

Trigonocarpus costatus sp. nov. (figs. 13-16)

DIAGNOSIS.—A radially symmetrical seed cast, elliptical in longitudinal section and circular in cross section. Sclerotesta (length 10 to 20 mm., width 7 to 10 mm.) slightly pointed at apex, rounded at base, and bearing on the surface three faint, equidistant ridges which extend from the base to the micropyle. Between the ridges occur about 20 faint striae, equally spaced, and running the entire length of the seed (figs. 13, 16).

This specimen resembles *Trigonocarpus multicarinatus* Newberry (5) in that it possesses a number of striae. These ridges are not so prominent as those of the latter species, and the larger ridges are not prolonged into the raised center of a cupped summit as in *T. multicarinatus*. *T. costatus* is slightly pointed at the micropylar end and not truncate as is *T. multicarinatus*.

This species (figs. 13-16) is represented by fourteen specimens, six of which were sectioned. There is considerable variation in size, and many of them were split into three equal valves along the line of the more prominent ridges (figs. 13, 14). Like the other casts, they bear a carbonized mass at the foramen which probably represents the continuation of the inner vascular elements. They are covered with a thin carbonized film representing the sarcotesta. The only other structure present is a membranous mass about 1 mm. inside the surface, which probably represents the megaspore membrane-nucellus complex.

Trigonocarpus serratus sp. nov. (fig. 17)

DIAGNOSIS.—A radially symmetrical seed, elliptical in longitudinal section and circular in cross section. Sclerotesta (length 14 mm., width 7 mm.) transformed at apex into a cup-like structure, 3 mm. high, which is divided into six equal, triangular teeth, each 2 mm. long. The body is 11 mm. in length, and bears on the surface indications of three faint, equidistant ridges, between which the surface is smooth. The base is rounded, and has a carbonized mass in the foramen which represents the continuation of the inner vascular elements.

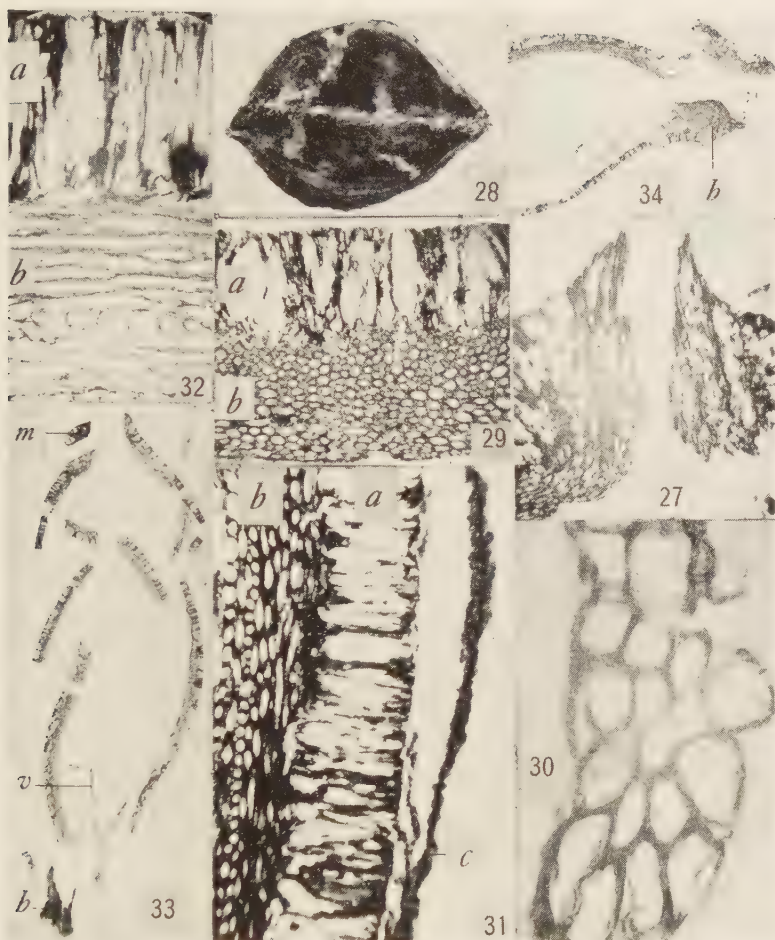
This species is represented by a single specimen, and was not sectioned. It differs from *Trigonocarpus ornatus* Newberry (5) in possessing only three faint ridges where that specimen bears six prominent ones, each of these being prolonged at the micropyle to form a division of the cup-like structure. In *T. serratus* the ridges, although opposite the lobes of the cup, appear to end with the main body of the seed and have no part in the formation of the cup. In *T. ornatus* the ridges are slightly constricted at the neck, and in the specimen studied there is a definite constriction between the cup-like summit and the body of the seed.

Sarcospermum ovale gen. et sp. nov. (figs. 27-36)

GENERIC DIAGNOSIS.—A radially symmetrical ovoid seed, circular in cross section, without ribs or sutures. Testa differentiated into three parts, sarcotesta, sclerotesta, and apparently an inner fleshy layer. Nucellus probably free to the base, and shows about 20 vascular strands in cross section.

SPECIFIC DIAGNOSIS.—Seed ovoid, 3 cm. long, with maximum width of 1.5 cm., circular in transverse section. Sarcotesta 0.04 mm. thick in its present crushed condition. Sclerotesta composed of outer palisade layer of thick walled cells 0.5 mm. in extent, and an inner layer (0.5 mm. thick) 13 to 18 elements wide of elongated fibrous cells. Sclerotesta slightly pointed at micropylar end and enlarged at basal end.

There is much similarity in the general plan of structure of the seeds of *Stephanospermum* Brongniart, *Actheotesta* Brongniart, and *Sarcospermum*. *Sarcospermum ovale* differs from *Stephanospermum*



FIGS. 27-34.—*Sarcospermum ovale* gen. et sp. nov. Fig. 27, near median section of micropyle showing short micropylar tube. Fig. 28, surface view of seed showing part of base covered by inclosing matrix; micropylar end to right. Fig. 29, portion of cross section of seed coat: *a*, palisade cells of outer portion of sclerotesta; *b*, inner layer of sclerotesta, composed of long, isodiametric, fiber-like cells. Fig. 30, cross section of vascular bundle of nucellar vascular tissue, a mesarch bundle composed of scalariform tracheids. Fig. 31, portion of near cross section of sarcotesta and sclerotesta: *b*, fibrous layer; *c*, remains of sarcotesta, split and crushed. Fig. 32, portion of longitudinal section of sclerotesta. Fig. 33, near median longitudinal section showing badly crushed condition of tissues: *m*, micropylar region; *v*, vascular elements of nucellus; *b*, portion of base. Fig. 34, median longitudinal section of base of seed.

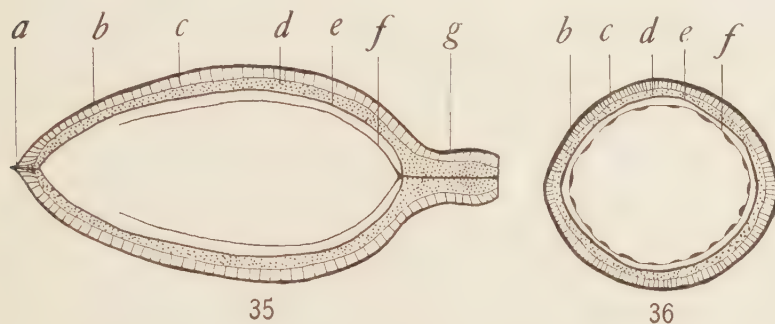
akenoides Brongniart in being of a much larger size, in lacking the long micropylar tube surrounded by a prominent crown, in having a much larger base, and in having the nucellar vascular elements divided into definite strands rather than being in a continuous sheath. *Sarcospermum ovale* differs from *Stephanospermum caryoides* Oliver (6) in being about twice the size of that specimen, in lacking the abbreviated crown, which has a hairy epidermis in the micropylar region, and in the structure of the nucellar vascular system as in *Stephanospermum akenoides*. In general structure *Sarcospermum ovale* approaches *Aetheotesta elliptica* Renault somewhat more closely than it does the other two species. *Sarcospermum ovale* differs from this specimen principally in having a much more enlarged base, and in possessing a sarcotesta which is of uniform thickness over the entire seed, rather than one that is much enlarged on both the basal and the micropylar ends and thin about the middle. The micropylar portion of the sarcotesta in *A. elliptica* is lacunose in nature, and the sclerotesta is prolonged into a micropylar tube. The nucellar vascular systems in *A. elliptica* and in *S. ovale* are divided into definite strands, but they appear to reach farther into the seed cavity in the latter.

This seed from Wilmington, Illinois, was so crushed and broken during the process of fossilization that it is difficult to determine accurately its former shape (fig. 33).

The sarcotesta was present over the entire seed, except at the micropylar canal, and is of uniform thickness. It was so crushed and decayed that it is impossible to determine its former thickness. This layer is split in places (fig. 31 c), and parts of it appear outside of a layer of calcite, about 1 mm. thick, which surrounds the seed.

The sclerotesta completely invests the seed except at the upper end where it is perforated by the micropylar canal (fig. 27). This tissue is composed of two distinct layers of cells. The outer is a single row of thick walled palisade-like cells which extend at right angles to the inner layer. These cells are about 0.5 mm. in length, and are of uniform thickness over the seed except at the micropylar and basal ends. In the region of the micropylar beak they are considerably elongated and gradually come to take a position nearly parallel to the vertical axis (figs. 27, 35 a). In the extreme basal

region these palisade cells are much elongated and are at an angle of about 30° to the longitudinal axis (figs. 34, 35). They are distinctly separated from the layer beneath, and are mostly filled with a carbonized, opaque substance. These palisade-like cells appear to be the outermost layer of the sclerotesta. The inner layer is composed of elongated thick walled cells which are isodiametric in cross section (figs. 29, 32). These cells extend lengthwise in the seed for the most part, but are often tortuous and twisted irregularly about one another, especially in the basal region (fig. 34). This tissue makes



FIGS. 35, 36.—Fig. 35, reconstructed median longitudinal section of seed: *a*, micro-pyle; *b*, remains of sarcotesta; *c*, palisade layer of sclerotesta; *d*, fibrous layer; *e*, inner flesh; *f*, vascular tissue of nucellus; *g*, large base of seed. Fig. 36, reconstructed cross section of middle of seed: *f*, nucellus showing about 20 vascular bundles.

up the greater part of the relatively large base of the seed, which is about 4 mm. long and 4 mm. thick below the body of the seed (fig. 34). The innermost layer of the sclerotesta is composed of the same elongated thick walled cells as the rest of the fibrous layer, and does not have the appearance of a definite epidermal layer.

There is no definite tissue which may be called the inner flesh, but there is a region just inside the sclerotesta which has a darker color and appears to be the debris from some tissue. This, and the fact that the sclerotesta has no finishing layer, or epidermis, would indicate that the inner flesh was present.

There is some question as to whether this seed shows a nucellus. At some distance inside the sclerotesta appears a definite membranous structure, which is much shrunken, and bears on its inner face about 20 definite vascular bundles. There are traces on the out-

side of this membranous structure of thinner walled tissue which has an amber colored material inside the cell walls. It cannot be determined definitely whether these belong to the integument or to the nucellus, but apparently they belong to the latter structure. The vascular bundles are made up of scalariform tracheids, and each bundle contains from a few of these elements to more than 25 (fig. 30). The bundles appear to be mesarch, with the smallest elements near the center of each bundle although it was not definitely determined whether these were protoxylem. The vascular system extends from the base of the seed cavity to a region in the neighborhood of the probable location of the pollen chamber. There are no vascular elements through the base of the seed, contrary to expectation, nor was a pollen chamber seen. There is no indication of any tissue inside of the nucellar vascular system.

Summary

1. A histological study was made of about 100 sandstone casts from the Lower Pennsylvanian strata of Arkansas, and one seed coat from Illinois.

2. Six species of the Trigonocarpales are described, five of them belonging to the genus *Trigonocarpus* Brongniart, and one being a new genus and species. The plants described are: *T. dawesi* Lindley and Hutton, *T. nocggerathi* Brongniart, *T. ouachitensis* Deevers, *T. costatus* Deevers, *T. serratus* Deevers, and *Sarcospermum ovale* Deevers.

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LITERATURE CITED

1. ARBER, E. A. N., A revision of the seed impressions of the British Coal Measures. Ann. Bot. 28:81-108. 1914.
2. CRONEIS, CAREY, Geology of the Arkansas Paleozoic area. Arkansas Geol. Surv. Bull. 3. 1930.

3. FIEDLER, HEINRICH, Die fossilen Früchte der Steinkohlen-Formation. Nova Acta Acad. Caes. Leop. Carol. Nat. Curio. 26: 241-296. 1857.
4. KRICK, HARRIETTE V., Structure of seedlike fructifications found in coal balls from Harrisburg, Illinois. BOT. GAZ. 93: 151-172. 1932.
5. NEWBERRY, J. G., Geol. Surv. Ohio 1: pt. 2. 1873.
6. OLIVER, F. W., On the structure and affinities of *Stephanospermum* Brgt., a new genus of fossil seeds. Trans. Linn. Soc. London. 2d Ser. 6: 361-400. 1903.
7. SALISBURY, E. J., On the structure and relationships of *Trigonocarpus shorensis* sp. nov. Ann. Bot. 28: 39-80. 1914.
8. SEWARD, A. C., Fossil plants. Cambridge. 1919.
9. SCOTT, D. H., Studies in fossil botany. 3d ed. Vol. II. London. 1920.
10. SCOTT, D. H., and MASLEN, A. J., The structure of the Paleozoic seeds, *Trigonocarpus parkinsoni* Brgt. and *Trigonocarpus oliveri*, sp. nov. Ann. Bot. 21: 89-134. 1907.

